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Modeling the Environmental and Seasonal Influence on Canopy Dynamic and Litterfall of Even-Aged Forest Ecosystems by a Model Coupling Growth & Yield and Process-Based Approaches

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***Abstract*—The aim is to propose a dynamic model of forest growth and biomass suitable to varied ecosystems with different species, soil types, climate conditions and forest managements. This model is combining different approaches (growth & yield, process-based and biogeochemical cycles) to take into account carbon, water and nutrient cycles and to include several processes such as wood production, transpiration, litterfall, litter decomposition or losses of nutrients by drainage. Such a model is necessary to anticipate and adapt forest management under different environmental and management scenarii (global changes).**

Considering the whole forest ecosystem, the seasonality of canopy dynamics and litterfall production is involved in key processes: photosynthesis and carbon production, stand transpiration and water cycle, litter decomposition and nutrient cycling. A dynamical probabilistic model for leaves demography has been created. This model is strongly constrained by environmental factors and is able to rank their influences. Model adjustment can highlight relationships between different scales of processes involved, from cellular-scale to stand-scale.

The aim is to provide: i) a predicting model suitable to a large range of ecosystems, ii) hierarchical analyses of the environmental processes driving canopy dynamics.

***Keywords*-Crop Models; Forest Growth Models; Dynamic Model; Stochastic Model; Adaptation to Climate Change; Forest Management; Process-Based Model (PBM); Leaf Ecology.**

I. Introduction

A better understanding of forest ecosystems functioning is motivated by climate changes, socio-economic and environmental constraints. This requires dynamical models of forest growth and biomass production suitable to varied ecosystems (species, soil, climate) and forest management (harvesting, fertilization). To date, the literature on the functioning of forest ecosystems is extensive enough to develop relevant models of forest ecosystems strongly influenced by mankind.

For example, congolese *Eucalyptus* plantations have been extensively studied over the last twenty years in terms of biomass dynamics, nutrient cycling [1], [2] and changes caused by the implementation of these monocultures in the congolese savannah [3]–[5].

Among models dedicated to the functioning of forest ecosystems, the empirical growth & yield (G&Y) model E-Dendro can predict for the growth and biomass accumulation for *Eucalyptus* monospecific plantations [6]–[8]. This model is based upon an adaptation of the empirical law of Eichhorn. At stand-level, it provides a solid support for modeling the growth & yield (G&Y) of monospecific plantations.

This category of model renders estimations of growth and biomass production related to stand age and fertility index. This index is specific for each study site, constant over time and does not take into account the influence of climate and soil variations. Then, it is difficult to anticipate the production of biomass under different environmental scenarii (global changes).

Based on the assumption that all forest ecosystems are governed by common processes of growth and interaction with the environment, it seems reasonable to propose a generic approach for their modeling. This requires the development of tools adapted to the characteristics of each ecosystem and respectful of the general processes of growth. In practice, we seek to extend the E-Dendro model to other species (oak, beech, pine), climates and sites. First of all, It leads to focus on the canopy dynamics as a key process of forest ecosystems growth, water cycle and nutrient cycling.

Designing the canopy and its interaction with environment pushes the modeler to combine G&Y and process-based approaches to take into account on growth, climate and soil. The main objective is to propose an inter-disciplinary enrichment instead of a juxtaposition of different equations or models.

II. Method & modeling approach

The whole model is dedicated to even-aged, monospecific plantations.

A. Growth and Yield model

The G&Y model provides a non-seasonal estimation of foliar biomass (Fig.1) which can be considered as the crop age effect on leaves production.

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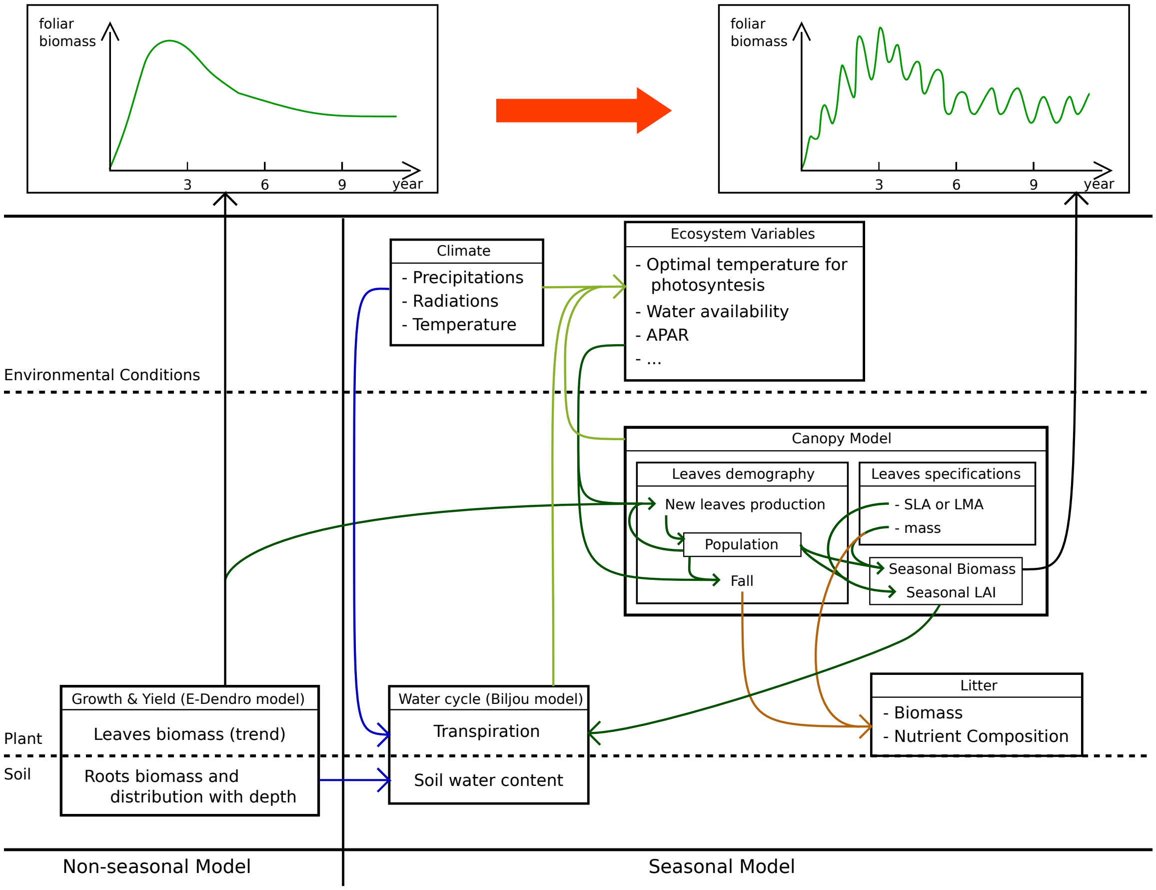


Figure 1. Scheme of model structure

The current estimation is based on the E-Dendro model [6]. This monthly model is relying on an adaptation of Eichhorn laws and is used to define silvicultural practices in *Eucalyptus* plantations.

The category of G&Y models is defined by a common principle. If the model is considered as a function, the relation (1) shows the main principles considered to estimate production:

$$\text{Production} = model(\text{Species}, \text{Site/Fertility Index}) \quad (1)$$

where: i) “Species” corresponds to parameters associated to genotypic part of the growth processes and ii) “Site/Fertility Index” (SFI) corresponds to climate, soil properties, nutrients and water availability.

In the current model, SFI is constant in time for each particular ecosystem. It is statistically determined on forest inventories and is non season-dependent.

B. Water cycle

The seasonal dynamics of water is a key factor of biomass production. Its prediction requires an association between a G&Y model and a process-based model for crop transpiration. The E-Dendro model and the Biljou model [9] are coupled for the study.

Biljou is a climate dependent model providing estimation of soil water availability, drainage and crop transpiration. Particularly, it can identify and estimate the drought periods. The Biljou model is described in details in [9]: water cycle is driven by leaf area index (LAI) ($m^2_{leaf}\ m^{-2}_{ground}$) which is the key variable for coupling the models. LAI is given by the canopy model. Thus, seasonal variations of LAI will impact the simulation of water cycle (Fig.1).

C. Seasonality & Production

According to the main objective, the new model must integrate environmental changes. If the model is considered as a function, eq.(1) moves as follows into eq.(2):

$$\text{Production} = model(\text{Species}, \text{Soil}, \text{Nutrient}, \text{Climate}) \quad (2)$$

where: i) “Soil” corresponds to the soil structure, ii) “Nutrient” corresponds to the nutrient availability and iii) “Climate” corresponds to various climatic data (irradiance, precipitation, temperature).

The paper is focusing on soil water and climate impact on the canopy dynamics (see III). The simulations of seasonal variations of biomass and LAI are based on the non-seasonal production estimation (Fig.1).

III. Canopy dynamic model

The step time used in the E-Dendro model is the month. Let k be the age of the plantation.

The canopy is considered as a population of leaves distributed in class of ages named cohorts. If a leaf is hold by the tree, its age corresponds to the holding period. If a leaf has fallen, its age is defined by the duration between its creation and its fall.

Each month, firstly we consider the fall probability of each leaf in each cohort and secondly the production of new leaves. Then, we define a probabilistic dynamic model for the canopy demography.

A. From a single leaf...

Let $i \in \mathbb{N}^*$ be the time variable associated to leaf age. Note that the age i of a leaf is always less than or equal to the stand age k.

1) Fall probability: The fall probability for a leaf of age i at month k is denoted as follows (Fig.2):

$$\mathbb{P}(\text{Fall}|i,k) = p_F^i(k) \tag{3}$$

This probability depends on leaf age, crop age and ecosystem variables (Fig.1).

Let $(p_j^i(k))_{j\in\{1,q\}}$ be q fall indexes. Each fall index is a real number in $[0,1]$ and is associated to a single environmental effect on leaf longevity (see Table I).

The probability $p_f^i(k)$ is then defined as follows:

$$p_F^i(k) = f(p_1^i(k), p_2^i(k), \ldots, p_q^i(k)) \tag{4}$$

where f is a combinatory function defined below.

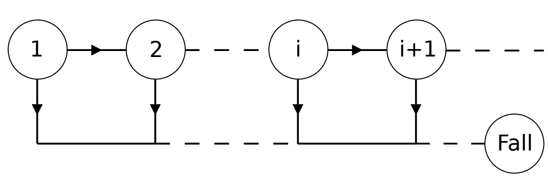


Figure 2. Individual leaf states (growth or fall)

In the following, the transition law for a leaf of age i at month k is denoted $\mathcal{L}_k^i$.

2) Combinatory function for q fall indexes: Let us define the function $f : [0,1]^q \to [0,1]$ by:

$$f(p_1^i, p_2^i, \ldots, p_q^i) = 1 - (1-p_1^i)(1-p_2^i)\ldots(1-p_q^i) \tag{5}$$

and satisfying:

if $p_1^i = 1$ or $p_2^i = 1 \ldots p_q^i = 1$, then $f(p_1^i, p_2^i, \ldots, p_q^i) = 1$.

i.e. when any fall index equals 1, the leaf falls.

B. ... to population

For each month, a "generation law of individuals" is defined as a $\mathbb{N}$-valued random variable N_k^1. It corresponds to the production of a new cohort of leaves. The population N_k of leaves carried by the crop at month k is given by:

$$N_k = \sum_{i\geq 1} N_k^i \tag{6}$$

where N_k^i is the number of leaves of age i.

The model can be considered as a branching process with immigration (fig.3) [10], [11]. Coupled with leave's morphological features such as surface (specific leaf area (SLA)) or mass, the model provides seasonal simulations on foliar biomass, litterfall and LAI (Fig.1).

IV. Hypothesis on leaf ecology

The formulation of both transition and generation laws arose from a review on leaf ecology literature.

The canopy turnover is considered as a combination of three successive processes: i) foliation/leaves production, ii) leaves growth and iii) scenescence/leaves fall.

The dominant theory is assuming that canopy turnover is triggered by optimization of forest growth and carbon-use efficiency [12], [13]. Thus, the optimization of carbon production and photosynthetic activity is the key of canopy dynamic. In this approach, each leaf owns a photosynthetic potential declining in time [14], [15]. If the leaf potential is lower than the cost to hold it, scenescence processes are initiated.

Independently from optimization theory, environmental stresses such as frost [16] or strong drought stress [12] can cause a premature leaf fall.

These considerations lead to a classification of the various climatic effects involved in leaf longevity: i) effects involved on carbon-balance optimization and ii) destructive effects on leave's components (see Table I).

Nutrients availability also plays an important role in the foliar dynamic [17]–[19]. These aspects are not considered yet. However, the modeling method may be extended without any limitation to nutrients effects.

Various ecosystems can be found along a latitudinal gradient [20] and the carbon-balance optimization is different from one ecosystem to another. Indeed, the processes involved in phenology depend on species and environmental conditions. To illustrate this point, we focused on two specifics ecosystems class: tropical evergreen and temperate deciduous.

A. Tropical evergreen ecosystems

In tropical ecosystems, the onset of phenological phases is driven by a combination of environmental factors, but the distinction of key processes involved is not clear [21]. For the monitored congolese *Eucalyptus* plantations we are working on, the processes are the following

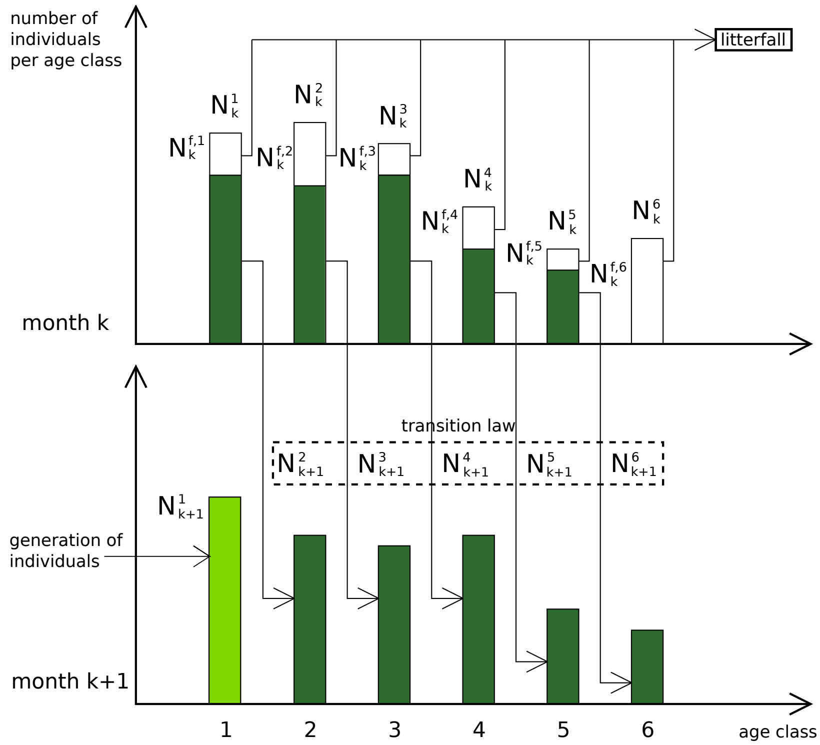


Figure 3. Leaves cohort dynamic

Foliation: The foliation of tropical species is mostly triggered by peaks of irradiance and changes in light regime. These phenomenon are associated to the change of seasons. Water availability is an additional limiting factor for the foliation [22]–[24].

Leaf fall: The leaves are hold until exhaustion of their photosynthetic potential [15], [21] thus a favorable light regime speeds up the fall [25]–[27]. The reduction of stomatal conductance during drought periods slows the photosynthetic activity and delays the leaves fall [13], [23]. Photosynthesis is enhanced during favorable temperature periods [23], [28].

B. Deciduous temperate ecosystems

In temperate climate, the foliation and the senescence of deciduous plantations are essentially triggered by photoperiod variations.

Foliation: When photoperiod drives foliation, the environmental influence is reduced to spring temperatures. A warm spring accelerates foliation processes. Photoperiod influence depends on altitudinal and temperature gradients. Water availability is also a limiting factor [29]–[32].

Leaf fall: Senescence processes are triggered by photoperiod and activated by temperatures: below a certain threshold, cold autumnal temperatures favor senescence. The photoperiod influence depends on altitudinal and temperature gradient [30]–[34].

V. Explicit formulations for Congolese *Eucalyptus* plantations

This part is developing a formulation for *Eucalyptus* stand.

A. Climatic & environmental variables

1) PAR absorption: The photosynthetic active radiation (PAR) absorption ($APAR$) stands for the monthly amount of energy available for photosynthesis. As explained in [35], the monthly energy available for the whole canopy $APAR$ at the month k is often expressed with the Beer-Lambert equation:

$$APAR(k) = PAR(k) \times (1 - exp(-K.LAI(k))) \quad (7)$$

where K is an extinction coefficient for the whole canopy. In order to quantify the fraction of APAR received by each cohort each month, we define at the month k for a cohort of age i:

$$APAR(i,k) = \frac{LAI(i,k)}{LAI(k)} \times APAR(k) \quad (8)$$

$$LAI(i,k) = N_k^i \times SLA(i,k) \times mass_{leaf}(i,k) \quad (9)$$

where $SLA(i,k)$ is the specific leaf area for a cohort of age i at the mont k and $mass_{leaf}(i,k)$ is the mass of a single leaf of age i at month k. The PAR index $I_{PAR}^i(k)$ at the month k for a cohort of age i is given by:

$$I_{PAR}^i(k) = \sum_{j=1}^{i} APAR(j, k-i+j) \quad (10)$$

Table I
A SHORT CLASSIFICATION OF CLIMATIC EFFECTS ON LEAF LONGEVITY

Climatic variable	*Carbon-balance optimisation*	*Destructive effects*
Water	Moderate drought: stomatal conductance reduction implies fall delay	Strong drought: cellular destruction
Radiations	i) High reception of PAR accelerate fall ii) Photoperiod variations trigger phenological phases	Sunburn
Temperature	Optimal photosynthetic temperature accelerates leaf fall	Destructive temperatures: frost effect, heat effect

2) Optimal photosynthetic temperature: The optimal temperature index $I^i_{T_{opt}}(k)$ at the month k for a leaf of age i is given by:

$$I^i_{T_{opt}}(k) = \int_{k-i}^{k} |T_{opt} - T(t)|dt \tag{11}$$

where T is the temperature and T_{opt} the optimal photosynthetic temperature.

3) Water availability stress: The water availability stress index $I^i_H(k)$ at the month k for a leaf of age i is given by (Fig.4):

$$I^i_H(k) = \int_{k-i}^{k} (REW_c - REW(t))^+ dt \tag{12}$$

where REW_c is a critical threshold associated to water availability and the function $(\,.\,)^+$ is defined by $(x)^+ = \max(0, x)$. This parameter derives from Biljou model [9] .

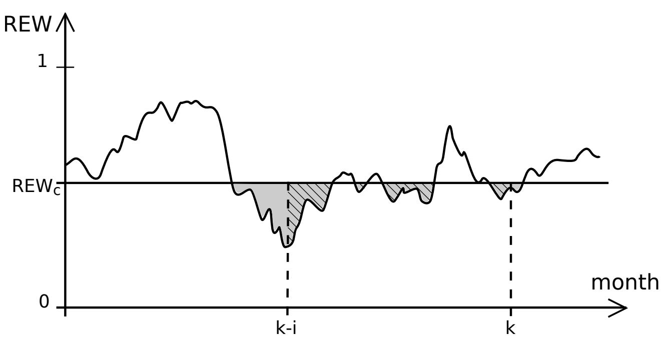


Figure 4. Water availability stress

B. Formulation of fall indexes

1) PAR fall index: $p^i_{PAR}(k)$ is given at the month k by the following two parameters formulation:

$$p^i_{PAR}(k) = 1 - e^{-\nu I^i_{PAR}(k)} \tag{13}$$

where $\nu > 0$ and is strongly related to the decline of photosynthetic rate A [21].

2) Optimal photosynthetic temperature fall index: $p^i_{T_{opt}}(k)$ is given at the month k by the following one parameter formulation:

$$p^i_{T_{opt}}(k) = p^{opt}_{T_{opt}} e^{-\alpha I^i_{T_{opt}}(k)} \tag{14}$$

where $p^{opt}_{T_{opt}} \in [0, 1]$ and $\alpha > 0$. For large value of $I^i_{T_{opt}}(k)$, the growth temperature is far from the optimal temperature and the trees delay leaf fall (Fig.5).

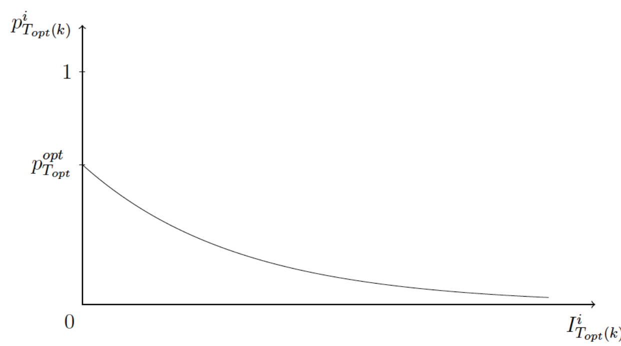


Figure 5. Optimal photosynthetic temperature fall index

3) Water availability delay stress fall index: $p^i_H(k)$ is given at the month k by the following two parameters formulation:

$$p^i_H(k) = \frac{H_{opt}}{H_{opt} + (1 - H_{opt})e^{rI^i_H(k)}} \tag{15}$$

where $H_{opt} \in [0, 1]$ and $r > 0$.

C. Formulation of the law of generation N^1_k

The monthly estimation of free space available for young leaves is named “monthly potential production of leaves” and is noted Θ. This potential is related to the trend of biomass B provided by the G&Y model. At month k, the potential is given by:

$$\Theta_k = \lfloor \lambda \frac{B_k}{\bar{m}} - \sum_{i=2}^{\infty} N^i_k \rfloor \tag{16}$$

where λ is a positive constant, $\bar{m}$ is the mean mass of a leaf and $\lfloor\ \rfloor$ is the nearest integer function.

The young leaves production is given by the combination of Θ and a "modulation function" depending on environmental parameters. The potential is reduced if environmental conditions are not favorable to foliation. According to the foliation in the tropics, we propose an expression for leaves production at month k:

$$N_k^1 = \lfloor \Theta_k \varphi(P_k, \Delta P_k) \rfloor \tag{17}$$

where φ is a two parameters $[0, 1]$-valued "modulation function" given by:

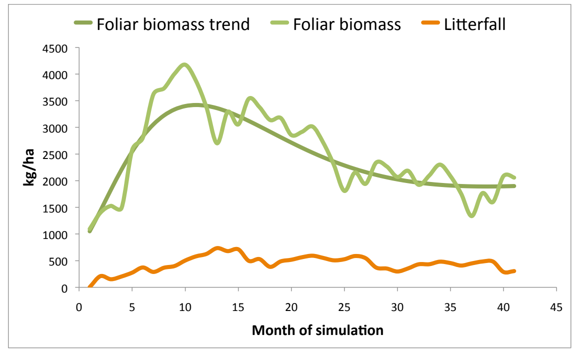
$$\varphi(P_k, \Delta P_k) = \frac{\omega P_k}{\omega P_k + e^{-\nu \Delta P_k}} \tag{18}$$

where ω and ν are positive constants, P are the monthly precipitations and ΔP are the variation of precipitations between two successive months. Leaf flushing appears mostly at the beginning of the wet season and is triggered by large variations in precipitation patterns.

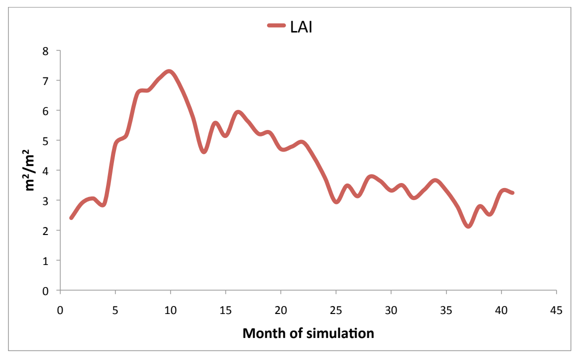
This formulation implicitly takes into account solar radiation. Indeed, the fall of leaves which have exhausted their photosynthetic potential is taken into account in the expression of Θ.

D. *Examples of simulation*

To illustrate the potential of the canopy model, we propose early simulations. Based on fictive climatic scenarii, arbitrary fall indexes parameters and experimental data for leaves features (mass and SLA), the canopy model produces foliar biomass, litterfall and LAI estimations for *Eucalyptus* plantations (Fig.6).



(a) Foliar biomass (trend & seasonal) and litterfall production



(b) Leaf Index Area

Figure 6. Simulations for a 5-month years old *Eucalyptus* stand under a fictive climatic scenario

VI. Conclusion

The theoretical model of canopy dynamics allows to consider a climate dependent estimation of the seasonal biomass production, combined with the empirical law for growth (Eichhorn law). Explaining the environmental factors involved in seasonal variations of canopy dynamic is a key step to identify their impact on the total crop growth.

This methodology differs from an usual statistical analysis. Indeed, the model is based on strong hypothesis on processes involved in leaf ecology. Through the study of experimental crop data such as soil water content, litterfall or LAI measurements, the most influential effects in canopy dynamics can be estimated for each particular ecosystem. This approach is defining a new field of investigation in the understanding of forest ecosystems.

VII. Perspectives

From a theoretical point of view, nutrients cycling is essential in ecosystem's growth and production. Including these aspects in a next modeling phase is necessary to give a new formulation of the site fertility index (Fig.7).

Defining generic families of fall indexes for specific species and comparing them through various study sites (eg: *Eucalyptus*) is necessary to provide an effective tool of modeling.

Due to the formalism modularity, the canopy dynamics model is suitable to various species, soil and climate. Thus, this model offers many perspectives in ecosystem's research such as the quantification of environmental effects on growth, what promises deepening their understanding.

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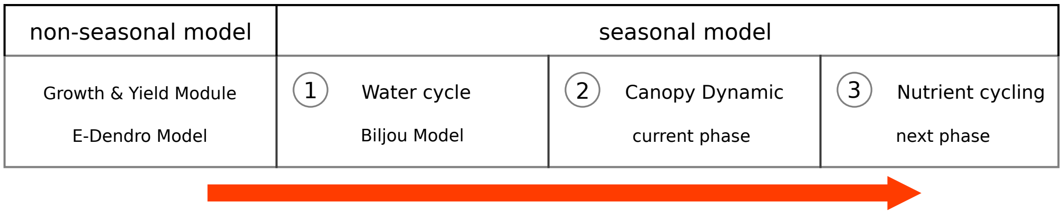

Figure 7. Modeling approach

REFERENCES

[1] J. P. Laclau, J. P. Bouillet, and J. Ranger, "Dynamics of biomass and nutrient accumulation in a clonal plantation of eucalyptus in congo," *Forest ecology and management*, vol. 128, no. 3, pp. 181–196, 2000.

[2] J. P. Laclau, P. Deleporte, J. Ranger, J. P. Bouillet, and G. Kazotti, "Nutrient dynamics throughout the rotation of eucalyptus clonal stands in congo," *Annals of Botany*, vol. 91, no. 7, pp. 879–892, 2003.

[3] J. P. Laclau, J. Ranger, J. P. Bouillet, J. D. Nzila, and P. Deleporte, "Nutrient cycling in a clonal stand of eucalyptus and an adjacent savanna ecosystem in congo 1. chemical composition of rainfall, throughfall and stemflow solutions," *Forest ecology and management*, vol. 176, no. 1-3, pp. 105–119, 2003.

[4] J. P. Laclau, J. Ranger, J. D. Nzila, J. P. Bouillet, and P. Deleporte, "Nutrient cycling in a clonal stand of eucalyptus and an adjacent savanna ecosystem in congo 2. chemical composition of soil solutions," *Forest ecology and management*, vol. 180, no. 1-3, pp. 527–544, 2003.

[5] J. P. Laclau, J. Ranger, P. Deleporte, Y. Nouvellon, L. Saint-Andre, S. Marlet, and J. P. Bouillet, "Nutrient cycling in a clonal stand of eucalyptus and an adjacent savanna ecosystem in congo 3. input-output budgets and consequences for the sustainability of the plantations," *Forest ecology and management*, vol. 210, no. 1-3, pp. 375–391, 2005.

[6] L. Saint-André, J.-P. Laclau, J.-P. Bouillet, P. Deleporte, A. Miabala, N. Ognouabi, H. Bailleres, Y. Nouvellon, and R. Moukini, "Integrative modelling approach to assess the sustainability of the eucalyptus plantations in congo," *Fourth Workshop*, 2002.

[7] L. Saint-Andre, A. T. M'bou, A. Mabiala, W. Mouvondy, C. Jourdan, O. Roupsard, P. Deleporte, O. Hamel, and Y. Nouvellon, "Age-related equations for above- and below-ground biomass of a eucalyptus hybrid in congo," *Forest ecology and management*, vol. 205, no. 1-3, pp. 199–214, 2005.

[8] L. Saint-Andre, J. P. Laclau, P. Deleporte, J. L. Gava, J. L. M. Goncalves, D. Mendham, J. D. Nzila, C. Smith, B. d. Toit, D. P. Xu, K. V. Sankaran, J. N. Marien, Y. Nouvellon, J. P. Bouillet, and J. Ranger, "Slash and litter management effects on eucalyptus productivity: a synthesis using a growth and yield modelling approach." *Site management and productivity in tropical plantation forests: Proceedings of workshops in Piracicaba (Brazil), 22-26 November 2004 and Bogor (Indonesia), 6-9 November 2006*, pp. 173–189, 2008.

[9] A. Granier, N. Breda, P. Biron, and S. Villette, "A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands," *Ecological Modelling*, vol. 116, no. 2-3, pp. 269–283, 1999.

[10] T. E. Harris, *The Theory of Branching Processes (Dover Books on Advanced Mathematics)*. Dover Pubns, 1963.

[11] P. Olofsson, "General branching processes with immigration," *Journal of Applied Probability*, vol. 33, no. 4, pp. 940–948, 1996.

[12] B. F. Chabot and D. J. Hicks, "The ecology of leaf life spans," *Annual Review of Ecology and Systematics*, vol. 13, pp. 229–259, 1982.

[13] K. Kikuzawa and M. Lechowicz, *Ecology of leaf longevity*, ser. Ecological Research Monographs. Springer, 2011.

[14] K. Kitajima, S. Mulkey, and S. Wright, "Seasonal leaf phenotypes in the canopy of a tropical dry forest: Photosynthetic characteristics and associated traits," *Oecologia*, vol. 109, no. 4, pp. 490–498, FEB 1997.

[15] K. Kitajima, S. Mulkey, M. Samaniego, and S. Wright, "Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species," *American Journal of Botany*, vol. 89, no. 12, pp. 1925–1932, DEC 2002.

[16] A. L. L. Silva, Y. da Oliveira, G. B. de Alcantara, M. de Santos, M. dos Quoirin, A. L. L. da Silva, Y. de Oliveira, G. B. de Alcantara, and M. dos Santos, "Chilling and frost tolerance in eucalypt leaves." *Biociencias*, vol. 17, no. 1, pp. 86–90, 2009.

[17] K. Hikosaka, "Leaf canopy as a dynamic system: Ecophysiology and optimality in leaf turnover," *Annals of Botany*, vol. 95, no. 3, pp. 521 – 533, FEB 2005.

[18] J. P. Laclau, J. C. R. Almeida, J. L. M. Goncalves, L. Saint-Andre, M. Ventura, J. Ranger, R. M. Moreira, and Y. Nouvellon, "Influence of nitrogen and potassium fertilization on leaf lifespan and allocation of above-ground growth in eucalyptus plantations," *Tree Physiology*, vol. 29, no. 1, pp. 111–124, 2009.

[19] A. Pornon, C. Marty, P. Winterton, and T. Lamaze, "The intriguing paradox of leaf lifespan responses to nitrogen availability," *Functionnal Ecology*, vol. 25, no. 4, pp. 796–801, AUG 2011.

[20] M. D. Lowman, "Leaf growth dynamics and herbivory in 5 species of australian rain-forest canopy trees," *Journal of Ecology*, vol. 80, no. 3, pp. 433–447, 1992.

[21] K. Kitajima, S. Mulkey, and S. Wright, “Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species,” *American Journal of Botany*, vol. 84, no. 5, pp. 702–708, MAY 1997.

[22] S. Wright and C. Van Schaick, “Light and phenology of tropical trees,” *American Naturalist*, vol. 143, no. 1, pp. 192–199, JAN 1994.

[23] C. Liu, C. Westman, B. Berg, W. Kutsch, G. Wang, R. Man, and H. Ilvesniemi, “Variation in litterfall-climate relationships between coniferous and broadleaf forests in eurasia,” *Global Ecology and Biogeography*, vol. 13, no. 2, pp. 105–114, MAR 2004.

[24] A. Huete, K. Didan, Y. Shimabukuro, P. Ratana, S. Saleska, L. Hutyra, W. Yang, R. Nemani, and R. Myneni, “Amazon rainforests green-up with sunlight in dry season,” *Geophysical Research Letters*, vol. 33, no. 6, MAR 2006.

[25] N. Osada, H. Takeda, A. Furukawa, and M. Awang, “Leaf dynamics and maintenance of tree crowns in a malaysian rain forest stand,” *Journal of Ecology*, vol. 89, no. 5, pp. 774–782, OCT 2001.

[26] P. Reich, C. Uhl, M. Walters, L. Prugh, and D. Ellsworth, “Leaf demography and phenology in amazonian rain forest: A census of 40 000 leaves of 23 tree species,” *Ecological Monographs*, vol. 74, no. 1, pp. 3–23, FEB 2004.

[27] G. Vincent, “Leaf life span plasticity in tropical seedlings grown under contrasting light regimes,” *Annals of Botany*, vol. 97, no. 2, pp. 245–255, FEB 2006.

[28] M. Battaglia, M. Cherry, C. Beadle, P. Sands, and A. Hingston, “Prediction of leaf area index in eucalypt plantations: effects of water stress and temperature,” *Tree Physiology*, vol. 18, no. 8-9, pp. 521–528, AUG-SEP 1998.

[29] F. Lebourgeois, J. C. Pierrat, V. Perez, C. Piedallu, S. Cecchini, and E. Ulrich, “Phenological timing in french temperate forests - a study on stands in the renecofor network.” *Revue Forestiere Francaise*, vol. 60, no. 3, 2008.

[30] Y. Vitasse, S. Delzon, E. Dufrene, J. Y. Pontailler, J. M. Louvet, A. Kremer, and R. Michalet, “Leaf phenology sensitivity to temperature in european trees: Do within-species populations exhibit similar responses?” *Agricultural and Forest Meteorology*, vol. 149, no. 5, pp. 735–744, 2009.

[31] Y. Vitasse, A. J. Porte, A. Kremer, R. Michalet, and S. Delzon, “Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology,” *Oecologia*, vol. 161, no. 1, pp. 187–198, 2009.

[32] Y. Vitasse, S. Delzon, C. C. Bresson, R. Michalet, and A. Kremer, “Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden,” *Canadian Journal of Forest Resarch - Revue canadienne de recherche forestière*, vol. 39, no. 7, pp. 1259–1269, 2009.

[33] N. Delpierre, E. Dufrene, K. Soudani, E. Ulrich, S. Cecchini, J. Boe, and C. Francois, “Modelling interannual and spatial variability of leaf senescence for three deciduous tree species in france,” *Agricultural and Forest Meteorology*, vol. 149, no. 6-7, pp. 938–948, 2009.

[34] Y. Fracheboud, V. Luquez, L. Bjorken, A. Sjodin, H. Tuominen, and S. Jansson, “The control of autumn senescence in european aspen,” *Plant Physiology*, vol. 149, no. 4, pp. 1982–1991, 2009.

[35] Y. . Nouvellon, A. . Begue, M. . . S. . Moran, D. . Lo Seen, S. . Rambal, D. . Luquet, G. . Chehbouni, and Y. . Inoue, “Par extinction in shortgrass ecosystems: effects of clumping, sky conditions and soil albedo.” *Agricultural and Forest Meteorology*, vol. 105, no. 1/3, pp. 21–41, 2000.